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BIOLOGY AND IMMATURE STAGES OF *OCHROTRICHIA FOOTEI* (TRICHOPTERA: HYDROPTILIDAE), A NEW MICROCADDISFLY FROM A TORRENTIAL MOUNTAIN STREAM

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Abstract.—The egg, larvae, pupa, and adult male of ***Ochrotrichia footei*, n. sp.**, taken from waterfalls in southern California are described. The species is univoltine, with early instars present during the summer months, and overwintering as fifth instars within their cases. First instars hatch from eggs deposited in abandoned pupal cases attached to vertical rock faces. Gut contents analysis and laboratory observations of living larvae indicate that larvae are scrapers of periphyton, including diatoms, green algae, cyanophytes, and fungal hyphae. The generalist trophic ecology of *O. footei* may be a preadaptation that allows this species to thrive in a harsh and variable environment.

Key Words: *Ochrotrichia footei*, microcaddisflies, new species, streams, larvae, scrapers, diatoms, Bacillariophyta, Cyanobacteria, Chlorophyta

The number of described species of microcaddisflies (Trichoptera: Hydroptilidae) from North America has been growing steadily during recent years (e.g., Harris and Sykora 1996, Moulton et al. 1999, Harris and Huryn 2000). *Hydroptila* and *Ochrotrichia* are the two most speciose genera with more than 50 and 100 species, respectively (Morse 1993), and most of the newly described species are placed in these genera. Despite efforts to catalog the species richness of the Hydroptilidae, the small size and often cryptic habits of the immature stages have created a lag in studies of their natural history and life cycles. Indeed, of the 300+ species from North America, larva/adult associations are known for only approximately 10% (Wiggins 1996, Keiper 1998, Keiper and Walton 1999).

Species of *Ochrotrichia* are found in lotic habitats (Wiggins 1996) where they are frequently associated with algal mats (Flint and Herrmann 1976; Keiper and Foote 1998, 1999, 2000; Keiper and Walton 2000) or surfaces of rocky substrate where they scrape periphyton (Vaillant 1984, English and Hamilton 1986). It appears that *Ochrotrichia* larvae are equipped with robustly cusped mandibles that allow them to either scrape relatively smooth substrates, macerate biofilms, or pierce cells within filaments of the green alga *Cladophora* (Vaillant 1984, English and Hamilton 1986, Keiper 1999, Keiper and Foote 2000, Keiper and Walton 2000). The only food sources reported for *Ochrotrichia* immatures are *Cladophora* and periphytic diatoms (Keiper and Foote 2000, Keiper and Walton 2000). Early instars do not build portable cases, whereas the fifth, and final, instar constructs either a bivalved purse-like case, or a dome-shaped case (Ross 1944, Wiggins 1996).

During the summer of 1999, *Ochrotrichia* adults of a new species were reared from larvae collected from a southern California stream. We describe the male, egg, larvae, and pupa, and give details on its natural history and feeding habits.

Materials and Methods

We collected larvae from Fullers Mill Creek in the San Bernardino National Forest of western Riverside County, near the city of Idyl Wild. Diatom-encrusted rock and algal mats were brought back to the laboratory with living larvae and placed in petri dishes or aerated rearing chambers (Keiper and Foote 1996). Periphyton was scraped with a knife and scooped into collecting vials to obtain early instars. Larval behavior and development was observed, and adults reared from pupae. All laboratory observations of living material were made at 20°C, and a 12:12 light:dark photoperiod maintained with incandescent lights.

Representative immature stages were fixed in Kahle's solution (Wiggins 1996) for 24 h and then preserved in 70% ethanol. Adults were placed directly in ethanol. Immatures were described following the methods of Keiper and Foote (1999). Because the case size for fifth instars varied between dates of collection, larvae and cases were measured separately for each date.

On 27 September 1999 and 18 May 2000, fifth instars were collected with forceps and placed directly into hot water carried in the field in an insulated thermos. After approximately 30 s, larvae were transferred to vials of 10% formalin for preservation. In the laboratory, formalin-preserved specimens were dissected, and the guts removed and smashed on a microscope slide with glycerin and a cover slip. The gut contents were described and enumerated for 5 larvae from May and 9 larvae from September. Descriptions of adults and larvae followed the terminology of Marshall (1979) and Wiggins (1996), respectively.

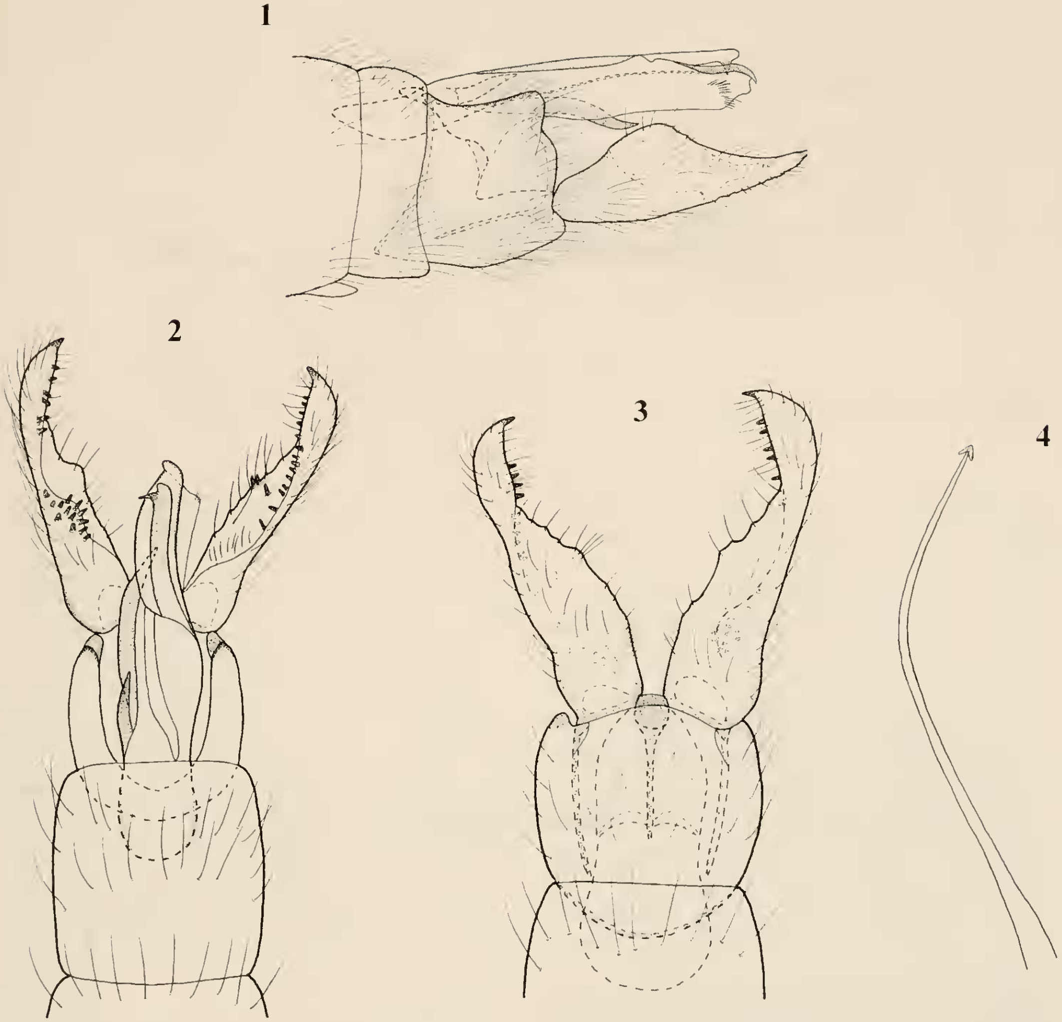
The collecting site, Fullers Mill Creek, is a low order, snow-melt stream. Due to the remoteness of the site and rugged terrain, the source was not found. The stream forms cobble-strewn channels and also cascades over bedrock, creating numerous waterfalls and madicoles. During the spring and early summer, the habitat is torrential and difficult to access. As the summer progresses and less snow-melt is available, the water slows to a trickle, and many areas bordering the stream remain wet from capillary action only. The green alga *Spirogyra* and the cyanophyte *Cylindrospermum* were visible in some areas, the red alga *Lemanea* was present at cascades, and rocky surfaces were frequently brownish-green with diatoms, unicellular green algae, and filamentous cyanophytes. Mosses were abundant at peripheral slash zones.

Larvae were collected from three waterfalls at approximately 1,800–1,900 m ASL, each with abundant mosses and diatoms. Each area had a central spill-way where most of the water ran, as well as lateral splash zones. Each area was open to the sunlight, and a variety of trees, mostly oaks (*Quercus* spp.) and pines (*Pinus* spp.), grew along the margins of the stream.

Results

Ochrotrichia footei Keiper and Harris, new species
(Figs. 1–4)

Adult male.—Length 3.5 mm. 31 antennal segments. Brown in alcohol. Abdominal segment VII with short ventromesal process; segment VIII ventrally angular; segment IX square in lateral view, reduced to narrow bridge dorsally (Fig. 1). Segment IX deeply incised mesally in dorsal view (Fig. 2), but rounded ventrally, with shallow lateral incisions posteriorly, a pair of lateral apodemes at outer juncture with inferior appendages (Fig. 3). Tenth tergum bearing several elongate processes, distally with narrow mesal process tipped with heavy spine subapically, anteriorly with pair of acute lateral processes on right margin, anteromost process short, posteromost process



Figs. 1–4. *Ochrotrichia footei,* male terminalia. 1, Lateral. 2, Dorsal. 3, Ventral. 4, Phallus.

elongate and curving inward (Fig. 2); in lateral view segment X thin and elongate, large spine basolaterally and ventrally, dorsal process ending in downward projecting spine, remainder of segment rectangular, with narrow, downward curving posterior sclerite, tuft of fine hairs laterad (Fig. 1); in ventral view with basomesal process, thin anteriorly and rounded posteriorly (Fig. 3). Inferior appendages in lateral view triangular, distally tapering to thin, sclerotized apex (Fig. 1); in dorsal view rectangular, with series of short pegs on inner margin, heavier spine at apex, right inferior appendage with lobe near base bearing numerous short pegs, left inferior appendage with several short pegs on inner margin near midlength (Fig. 2); in ventral view wide basally, tapering to midlength, distally rounded on outer margins, with short pegs on inner margin (Fig. 3). Phallus tubular and thin, small triangle at apex (Fig. 4).

Diagnosis.—*Ochrotrichia footei* appears to be most similar to *O. salaris* Blickle and Denning in the overall configuration of tergum X. Both species have an elongate mesal process which terminates in a lateral spine, and both species have a pair of lateral

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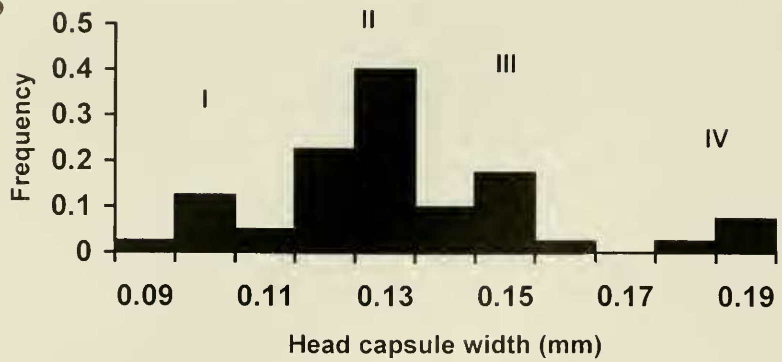


Fig. 5. Histogram of head capsule width for field-collected early instar *Ochrotrichia footei* (n = 40). Numbers placed over peaks indicate estimated instar.

processes. However, the inferior appendages of the new species are triangular in lateral aspect, more similar to those of *O. mono* (Ross) than to those of *O. salaris*, which are narrow at midlength and bear heavy spines from the ventral margin, both anteriorly and posteriorly. The features of the tenth tergum in combination with the shape of the inferior appendages will serve to readily identify *O. footei*.

Type material.—Holotype, ♂: United States, California, Riverside County near Idyl Wild, Fullers Mill Creek, reared from larva collected 29 June 1999, emerged 7 July 1999, J. B. Keiper; deposited at the Cleveland Museum of Natural History, Department of Invertebrate Zoology. Paratypes: 1 ♂, 4 ♀, same location as holotype, except reared from larvae collected 27 June 1999, J. B. Keiper; 2 ♂ pupae, collected 3 July 2000, J. B. Keiper. Paratypes deposited with holotype male, except for 1 male and 2 females (27 June 1999) deposited at the National Museum of Natural History, Smithsonian Institution, Washington, DC.

Egg.—Round, chorion colorless, no surface markings evident; embryo bright yellow, developing dark brown to black eye spot with age. Maximum diameter 0.20–0.23 mm ($\bar{x}$ = 0.21 mm). (n = 10).

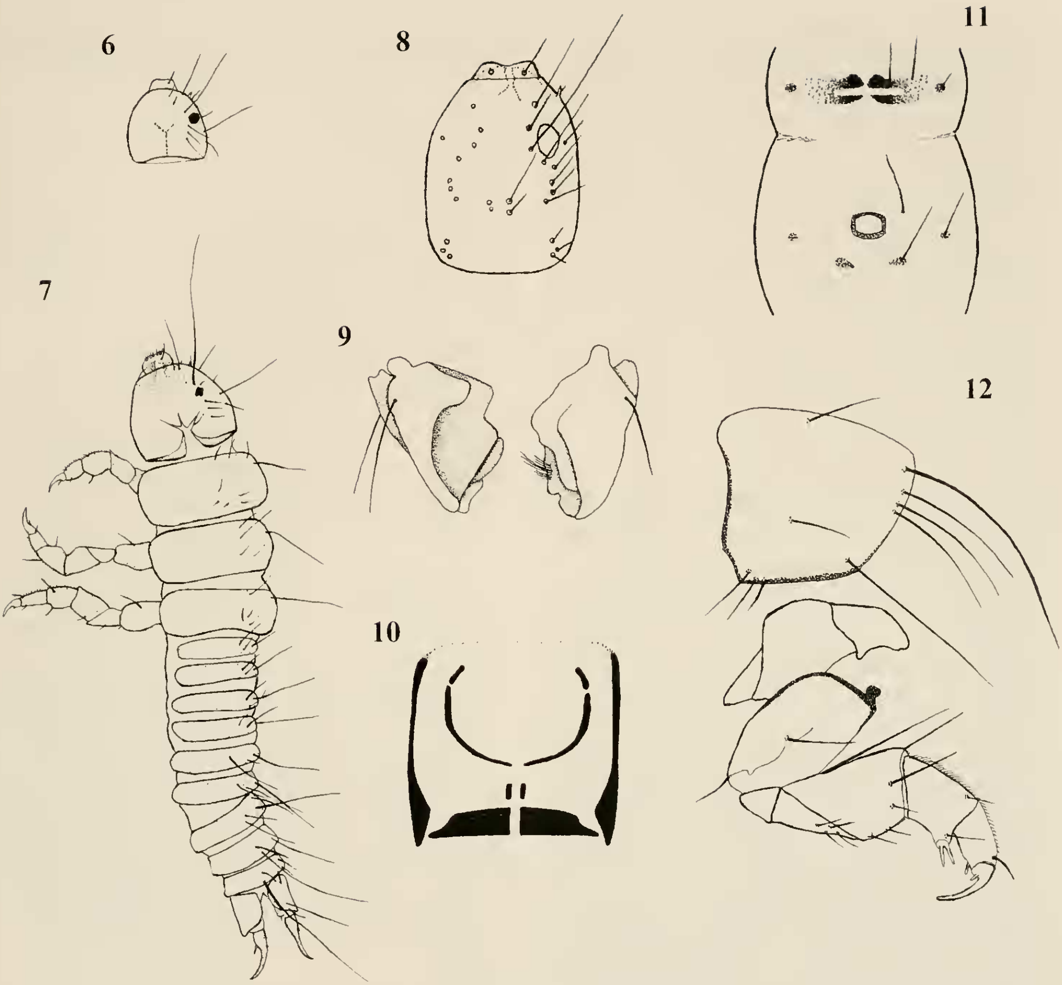
Larvae.—Except for field-collected fifth instars and first instars obtained from eggs in the laboratory, determination of larval stadium was only possible by measuring the head capsule width of field material (n = 40 early instars). Using peaks in a histogram we approximated head capsule width (Fig. 5). Instars 1-4 without cases, as is typical for Hydroptilidae (Wiggins 1996).

First instar: Flattened dorsoventrally, non-sclerotized areas of body white, nearly transparent. Head: width 0.09–0.10 mm, pale brown, posterior margin with thin brown band, sutures evident, newly hatched larvae lacking coloration except for primary setae and eye spot (Fig. 6). Thorax: sclerites pale brown, primary setae well developed. Abdomen: dorsal sclerites rectangular, covering most of dorsum of each segment; segment 10 bifurcate, bearing large anal claws. (n = 10).

Second instar: Similar to first instar, just differing in size and proportions of body parts; sclerites darkening with age. (n = 10).

Third instar: Sclerites darkening considerably. Head: Primary seta near eye spot long, 1.5× length of head capsule, otherwise similar to first instar. Thorax: One pair of long setae laterally on each notal sclerite, others small and weak. Abdomen: Three pairs of strong setae laterally; dorsal sclerite on segment 9 with one pair of long setae positioned mesad, subequal in length to primary seta near eye spot. Otherwise similar to first instar except in size and proportion (Fig. 7). (n = 10).

Fourth instar: Similar to third instar, dif-



Figs. 6–12. *Ochrotrichia footei*, larvae. 6, Head capsule of first instar, right side only with setation. 7, Slide-mounted third instar, dorsal view, right side only with setation, left side only with thoracic legs; note damage to posterior of head capsule and flattening of body a result of slide preparation. 8, Head capsule of fifth instar, right side only with setation. 9, Fifth instar, mandibles, ventral view. 10, Fifth instar, prosternal sclerites, legs removed. 11, Fifth instar, abdominal segments 1 and 2, dorsal view. 12, Fifth instar, pronotal sclerite and fore leg, lateral view.

fering only in size and proportions of body parts, sclerites uniformly dark brown. (n = 4).

Fifth instar: Shape and coloration typical of *Ochrotrichia*, head and thoracic segments mostly dark brown, grading to black or tan in some areas. Head: width 0.15–0.19 mm ($\bar{x}$ = 0.17 mm); eye spot round, black, surrounded by narrow pale ring ca. 0.015 mm wide; position of primary setae as in Fig. 8; longest seta near eye spot approximately same length as head; anterior edge of labrum slightly concave in dorsal view; antenna short, with narrow base, bearing short seta approximately same length as base; right mandible bearing one seta on posterolateral corner, left mandible bearing two (Fig. 9); left mandible with row of hair-like setae on inner margin among dentition; mandibles asymmetrical, each robustly cusped. Thorax: prosternal sclerites dark brown, anterior sclerite small, rectangular, and divided by thin membranous area, two posterior sclerites narrowing laterally, truncate medially (Fig. 10); each sclerite mostly dark brown, with anterior margin lined with dark setae curving anteroventrad; notum with black posterior and lateral margins, black area extending somewhat along anterior margin in darker specimens, never wider than 0.05 mm; legs dark brown to black, foreleg 0.30 mm, midleg 0.36 mm, and hindleg 0.36 mm, leg ratio 0.83:1.00:1.00; fore tibia and tarsus with anterior margin lined with short hairs, fore tibia with strong ventral projection bearing stout setae, tarsal claw curved with short basal seta (Fig. 12); mesothoracic sclerite with black anterolateral corner; metathoracic sclerite with anterolateral corner produced, tan laterally. Abdomen: milky white, approximately 3.0–3.5× as wide as thorax in lateral view, approximately 2.0× as wide as thorax in dorsal view, somewhat compressed laterally; brown sclerotized rings dorsally on segments 2–8 (Fig. 11), rings on segments 2–4 oblate with lateral edges truncate, rings on segments 5–8 more rounded; segment 1 with dorsal sclerite divided by central membranous band, sclerite fading to pale color laterally; sclerites on abdominal segments 9–10 uniformly dark brown, anal claw somewhat lighter brown than other sclerites, approximately 0.01 mm long; case comprised of minute sand grains in two purse-shaped valves, typical of that for *Ochrotrichia* (Wiggins 1996). (n = 10, mature fifth instars only).

Newly molted fifth instars bear sclerites that are somewhat lighter brown than mature larvae. The dorsomedial sclerite of abdominal segment 1 is less extensive and difficult to see. Otherwise, these young fifth instars are similar except that the abdomen is not swollen and approximately the same girth as the thoracic segments. Length of larvae taken in June were 2.47–4.34 ($\bar{x}$ = 3.31) mm, while those taken in September measured 1.46–3.07 ($\bar{x}$ = 2.12) mm; cases collected in June were 3.21–4.18 ($\bar{x}$ = 3.68) mm in length and contained mature larvae, whereas those cases collected in September contained smaller larvae, and were 1.10–2.04 ($\bar{x}$ = 1.61) mm in length.

Pupa.—Typical of Hydroptilidae; 2 ♂, length 2.7 and 2.9 mm. No distinguishing characters.

Etymology.—Named for Dr. Benjamin A. Foote, Professor Emeritus, Kent State University, who introduced the senior author to Hydroptilidae, in honor of his many contributions to aquatic entomology.

Biology.—One female was observed to emerge on 27 September 1999 from the face of a waterfall. The pharate adult slid down a shallow film of water running over the rock face. After travelling about 20 cm, the adult broke free and flew to mosses adjacent to the water; the exuvia continued to move downward and was lost. The adult sat motionless for approximately one minute, took wing, and was collected with an aerial net. Three other adult females were observed on the same day walking over a water film, each dragging its ovipositor over the water. No oviposition was noted, nor were eggs located during a search of the rock face. Two of the females were collected, brought back to the laboratory alive, and placed in petri dishes with moist diatom-covered rocks. No oviposition occurred.

On 6 July 1999, an empty pupal case was found to contain approximately 50 eggs. The eggs adhered to each other forming a mass within the pupal case. Four more cases with similar egg masses were collected on 27 September. The eggs collected 27 September were placed in a petri dish with stream water and small pieces of diatom-covered rock; the eggs hatched two days later. Although larvae appeared to feed by scraping the substrate, no growth occurred. All larvae died within 5 d. Because only field collected eggs have been studied, the incubation period remains unknown.

In the field, active fifth instars were restricted to areas of noticeable water flow, rather than the wet margins of the waterfalls. Early instars were too small for field

Table 1. Algal and cyanobacterial taxa found in the guts of *Ochrotrichia footei* fifth instars taken in May and September.

Genus	Division	Month Collected May	September
Cocconeis	Bacillariophyta	X	X
Cymbella	Bacillariophyta	X	X
Diatoma	Bacillariophyta	X	
Epithemia	Bacillariophyta	X	
Gomphonema	Bacillariophyta	X	
Surirella	Bacillariophyta		X
Synedra	Bacillariophyta	X	X
Chlamydomonas	Chlorophyta	X	
Oedogonium	Chlorophyta		X
Anabaena	Cyanobacteria		X
Chroococcus	Cyanobacteria	X	
Phromidium	Cyanobacteria	X	
Pseudanabaena	Cyanobacteria	X	
Trachelomonas	Euglenophyta	X	

observations, but scrapings of algal films from areas of flowing water contained early instars while scrapings from wet margins lacked them. Only fifth instars that had attached their cases prior to pupation, or that had temporarily attached their cases to the rock to facilitate case-building efforts, were found in the thin water film at the margins of waterfalls.

Fifth instars brought back to the laboratory scraped diatom covered rocks placed in petri dishes and rearing chambers, but did not form pupae. Three field-collected pupae produced adults (2 ♂, 1 ♀) after ≥10 days. Larvae did not survive long enough in the laboratory for detailed observations of feeding habits.

Gut contents analysis revealed that diatoms were the most common item ingested, and ranged in size from 2.0–20.8 microns in length. Most diatoms were fragmented. Larvae collected in September never had more than 10 diatoms in their guts, whereas those collected in May contained 32–210 diatoms. Eleven algal and cyanophyte taxa were found in the guts of specimens from May, while only six were identified in September samples (Table 1). Fungal hyphae were present in specimens only in May.

Pupae formed aggregations in the field, and were often too numerous to count. All pupal cases were oriented parallel to the direction of water flow. During October 1999 visits to the stream, the rock substrates remained moist only in limited areas and many pupal cases were dry. Collections showed that no cases supported eggs, larvae, or pupae. A number of cases exhibited holes in one lateral valve, possibly made by the predatory behavior of an undetermined species of *Rhyacophila* (Rhyacophilidae) that inhabited the waterfall areas.

Discussion

Fifth instars are separated from all other known *Ochrotrichia* larvae by the combination of uniformly dark brown sclerites, narrow ring around eye spots, left mandible with two posterolateral setae, right mandible with one posterolateral seta, prosternal sclerites separated by a median gap, mediodorsal abdominal sclerites of segment I with longitudinal membranous band, abdominal segments II–VIII bearing mediodorsal ring sclerites with membranous centers, and cases purse-shaped bearing two lateral valves. Immatures are probably restricted to waterfalls or madicolous habitats, which is not uncommon for hydroptilid species (e.g., Ross 1944, Vaillant 1984, Wells 1985, Keiper and Walton 2000).

Much of the life history appears similar to that described for other *Ochrotrichia* spp. (Flint and Herrmann 1976, Vaillant 1984, English and Hamilton 1986, Keiper and Walton 2000). Certain species of Hydroptilidae have been reported to be intimately associated with filamentous algae as piercer/herbivores (Nielsen 1948; Keiper and Foote 1998, 1999, 2000), but *O. footei* never exhibited the algal piercing habit. Waterfalls that range from torrential to virtually dry may preclude populations of Hydroptilidae that exhibit specific trophic habits (e.g., Resh and Houp 1986; Keiper et al. 1998; Keiper and Foote 1998, 2000), thus the relatively generalized feeding habits may have preadapted *O. footei* for existence at Fullers Mill Creek. The mandibles appear well-suited for attacking rock substrates, and allow larvae to consume a variety of materials, similar to that of *O. quadrispina* (Keiper and Walton 2000). There appeared to be a dietary shift from May to September as more diatoms were consumed and a greater number of algal/cyanophyte taxa were present in guts during that period of greatest water flow. During May, three cyanophyte genera were present in guts, whereas *Anabaena* was the only cyanophyte taxon present in September. The green alga *Oedogonium* was the only chlorophyte consumed during late summer, and has been reported as a food source of the hydroptilid *Oxyethira arizona* Ross (Keiper and Walton 1999). The dietary shift was probably not behavioral, but resulted because of a change in the periphyton community as the habitat dried. These observations suggest that categorizing macroinvertebrates into functional feeding groups based on gut contents analysis may lead to spurious results if such analyses are taken from specimens collected from only one time period.

We can infer certain biological details based on laboratory and field observations. *Ochrotrichia footei* is probably univoltine and overwinters as fifth instars. Adults are active during summer months and multiple cohorts of immatures coexist. Small fifth instars with short cases are present in the autumn, and overwinter inside their cases. Larvae seal their cases in preparation for pupation after case building and growth are concluded in the spring. Due to the remoteness of the area, difficulty associated with field observations in torrential streams, and difficulty with rearings, many biological details remain unknown.

A particularly fascinating aspect of the biology of *O. footei* is that females place their eggs in one mass inside of empty pupal cases. Based on laboratory and field observations, it is evident that females leave their cases; parthenogenesis has never been reported in Trichoptera to our knowledge. After mating, females then must find a suitable case for egg deposition. All six cases with eggs were undamaged, and open to the environment through the apical slit in the case formed by escaping pharate adults. Few observations of hydroptilid oviposition have been recorded (but see Nielsen 1948, Resh and Houp 1986, Ito 1997), but some species do create egg masses. The behavioral adaptation of inserting eggs into attached cases may provide certain benefits, such as protection from desiccation, ultraviolet light, predators, or torrential waters.

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Literature Cited

English, W. R. and S. W. Hamilton. 1986. The larva of *Ochrotrichia arizonica* (Trichoptera: Hydroptilidae) with notes on distribution and geographic variation. Journal of the Kansas Entomological Society 59: 474–479.

Flint, O. S. and S. J. Herrmann. 1976. The description of, and environmental characterization for, a new species of *Ochrotrichia* from Colorado (Trichoptera: Hydroptilidae). Annals of the Entomological Society of America 69: 894–898.

Harris, S. C. and A. D. Huryn. 2000. New and rare microcaddisflies (Trichoptera: Hydroptilidae) from the eastern United States. Entomological News 111: 77–83.

Harris, S. C. and J. L. Sykora. 1996. New species of microcaddisflies from the eastern United States (Insecta: Trichoptera: Hydroptildiae). Annals of the Carnegie Museum 65: 17–25.

Ito, T. 1997. Oviposition preference and behavior of hatched larvae of an oligophagous caddisfly, *Palaeagapetus ovatus* (Hydroptilidae: Ptilocolepinae), pp. 177–181. *In* Holzenthal, R. W. and O. S.

Flint, eds. Proceedings of the 7th International Symposium on Trichoptera. Ohio Biological Survey, Columbus.

Keiper, J. B. 1998. Biology, larval feeding habits, and resource partitioning by microcaddisflies (Trichoptera: Hydroptilidae). Ph.D. Thesis, Kent State University, Kent, Ohio. 146 pp.

———. 1999. Morphology of final instar *Ochrotrichia xena* (Trichoptera: Hydroptilidae). Entomological News 110: 231–235.

Keiper, J. B., D. A. Casamatta, and B. A. Foote. 1998. Use of algal monocultures by larvae of *Hydroptila waubesiana* and *Oxyethira pallida* (Trichoptera: Hydroptilidae). Hydrobiologia 380: 87–91.

Keiper, J. B. and B. A. Foote. 1996. A simple rearing chamber for lotic insect larvae. Hydrobiologia 339: 137–139.

———. 1998. Biological Notes on *Ochrotrichia xena* (Ross) (Trichoptera: Hydroptilidae), a species newly recorded for Ohio. Proceedings of the Entomological Society of Washington 100: 594–595.

———. 1999. Biology and immature stages of two species of *Hydroptila* Dalman (Trichoptera: Hydroptilidae) which consume *Cladophora* (Chlorophyta). Proceedings of the Entomological Society of Washington 101: 514–521.

———. 2000. Biology and larval feeding habits of coexisting Hydroptilidae (Trichoptera) from a small woodland stream in northeastern Ohio. Annals of the Entomological Society of America 93: 225–234.

Keiper, J. B. and W. E. Walton. 1999. Biology and morphology of the mature larva of *Oxyethira arizona* Ross (Trichoptera: Hydroptilidae). Pan-Pacific Entomologist 75: 212–220.

———. 2000. Biology and immature stages of *Ochrotrichia quadrispina* Denning and Blickle (Trichoptera: Hydroptilidae), a spring-inhabiting scraper. Proceedings of the Entomological Society of Washington 102: 183–187.

Marshall, J. E. 1979. A review of the genera of the Hydroptilidae (Trichoptera). Bulletin of the British Museum of Natural History 39: 135–239.

Morse, J. C. 1993. A checklist of the Trichoptera of North America, including Greenland and Mexico. Transactions of the American Entomological Society 119: 47–93.

Moulton, S. R., S. C. Harris, and J. P. Slusark. 1999. The microcaddisfly genus *Ithytrichia* Eaton (Trichoptera: Hydroptilidae) in North America. Proceedings of the Entomological Society of Washington 101: 233–241.

Nielsen, A. 1948. Postembryonic development and biology of the Hydroptilidae. Det Kongelige Danske videnskabernes selskabs Biologiske Skrifter 5: 1–200.

Resh, V. H. and R. E. Houp. 1986. Life history of the caddisfly *Dibusa angata* and its association with the red alga *Lemanea australis*. Journal of the North American Benthological Society 5: 28–40.

Ross, H. H. 1944. The caddisflies, or Trichoptera, of Illinois. Bulletin of the Illinois Natural History Survey 23: 1–326.

Vaillant, F. 1984. The hydroptilid larvae of dripping rocks, pp. 407–412. *In* Morse, J. C. ed., Proceedings of the 4th International Symposium on Trichoptera. Series Entomologica 30, Dr. W. Junk Publ., Boston.

Wells, A. 1985. Larvae and pupae of Australian Hydroptilidae (Trichoptera), with observations on general biology and relationships. Australian Journal of Zoology, Supplementary Series 113: 1–69.

Wiggins, G. B. 1996. Larvae of the North American caddisfly genera (Trichoptera), 2nd Ed. University of Toronto Press, Toronto. 457 pp.